COMPARISON OF THE ANTARCTIC
AND ARCTIC FISH FAUNAS [*]

by

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ABSTRACT. - The Antarctic and Arctic fish faunas differ in age, endemism, taxonomic diversity, zoogeographic distinctiveness and physiological plasticity. The Antarctic fauna includes 274 species representing 49 families; the Arctic fauna 416 species in 96 families. Using 5% as a figure for recognition of dominant faunal elements, five groups account for about 74% of the Antarctic fauna (notothenioids, myctophids, liparids, zoarcids and gadiforms). With 35% of the species, notothenioids prevail in this assemblage. Together with the liparids, they are the only known example of an adaptive radiation of fish in a marine habitat. In the Arctic, six dominant groups comprise 58% of the fauna (zoarcoids, gadiforms, cottids, salmonids, pleuronectiforms and chondrichthyans). In the coldest water at the highest latitudes (> 65°S or N), only zoarcids and liparids are shared by both faunas. In the Antarctic species, endemism is 88% for the benthic fauna of the shelf and upper slope (174 species) and rises to 97% when only notothenioids are considered. Comparable figures in the Arctic are 20-25% for marine fish and 2% or less for freshwater and anadromous species. The high endemicity in the Antarctic reflects the isolation and age of the ecosystem: 22 million years versus only 0.7-2.0 million years for the Arctic. The Arctic fauna consists of boreal marine and freshwater fish which are generally more eurythermal and euryhaline than their Antarctic counterparts. The North Atlantic and North Pacific character of the marine fauna reflects the continuity of shelf areas between the Arctic and boreal regions. There are examples of convergent evolutionary trends in Antarctic and Arctic species that share habitat similarities. These trends are evident at several levels of diversity: intraspecific (genetic), specific (organismal) and ecological.

RÉSUMÉ. - Comparaison entre les faunes de poissons de l'Antarctique et de l'Arctique.

Les faunes de poissons antarctiques et arctiques diffèrent du point de vue de leur ancienneté, de l'endémisme, de la diversité taxinomique, de leur répartition géographique et de leur adaptabilité physiologique. La faune antarctique comprend 274 espèces appartenant à 49 familles; la faune arctique regroupe 416 espèces de 96 familles. En prenant un pourcentage de 5% comme valeur représentative d'un groupe dominant, cinq groupes principaux composent 74% de la faune antarctique (Notothenioidei, Myctophiformes, Liparidae, Zoarcoidei et Gadiformes). Avec 35% des espèces, les Notothenioidei sont le groupe dominant de cette faune. Avec les Liparidae, ils sont les seuls exemples de radiation adaptative de poissons en milieu marin. Dans l'Arctique, six groupes dominent et représentent 58% de la faune (Zoarcoidei, Gadiformes, Cottidae, Salmoniformes, Pleuronectiformes et Chondrichtyens). Dans les eaux les plus froides aux plus hautes latitudes (> 65°S ou N), seuls les Zoarcidae et Liparidae sont présents dans les deux hémisphères. Chez les espèces antarctiques, l'endémisme est de 88% pour la faune benthique du plateau continental et de la partie supérieure du talus continental (174 espèces) et s'élève à 97% si les Notothenioidei sont seuls considérés. Les chiffres analogues pour l'Arctique sont 20-25% pour les poissons marins et 2% ou moins pour les espèces d'eau douce ou anadromes. La haute endémicité dans l'Antarctique reflète l'isolement et l'âge de cet écosystème: 22 millions d'années contre 0,7-2,0 millions d'années pour l'Arctique. La faune arctique est

formée de poissons marins et d'eau douce boréaux qui sont généralement plus eurythermes et euryhalins que leurs homologues antarctiques. Les caractéristiques de la faune marine de l'Atlantique nord et du Pacifique nord reflètent la continuité qui existe entre les plateaux continentaux des régions arctiques et boréales. Il existe des exemples de tendances évolutives convergentes chez les espèces antarctiques et arctiques qui utilisent des habitats similaires. Ces tendances sont évidentes à plusieurs niveaux de diversité: intraspécifique (génétique), spécifique et écologique.

An evolutionary theme unites the research projects conducted by members of the Fishes of the Antarctic Ocean Network of the European Science Foundation. A logical extension of this evolutionary perspective includes a comparison of the fish faunas from both polar regions. Although the Antarctic fauna currently receives much attention, Arctic and boreal fishes served as subjects for some of the pioneering studies in low temperature fish physiology especially freezing resistance (Scholander *et al.*, 1957) and cold adaptation (Wohlschlag, 1957). Although there are convergent organismal and organ system adaptations to certain habitats and to physical and biological parameters, in many respects the Antarctic and Arctic faunas are more dissimilar than similar. If the late Cretaceous is taken as ground zero when there were no polar ecosystems and little biotic provincialization of the world's marine fish fauna, regional historical differences during the Cenozoic have resulted in modern polar faunas of contrasting age, endemism, taxonomic diversity, zoogeographic distinctiveness and physiological plasticity.

There are several advantages in using fish from both poles for comparative studies. It allows data to be viewed in a broader phylogenetic and ecological perspective. It also affords a greater degree of certainty when invoking a common environmental parameter as the possible basis for an adaptation. Given that the two faunas are largely composed of unrelated fish, they also permit examination of convergent evolutionary trends to similar environmental conditions at levels of biological organization ranging from the molecule to the organism. In this paper, I will compare the polar faunas with emphasis on 1) higher taxonomic composition and 2) convergent evolutionary trends at various levels of diversity in Antarctic and Arctic species that share some habitat similarities.

THE POLAR REGIONS

Historical

The geography, oceanography, biology and evolution of the two polar ecosystems have been compared numerous times (Dunbar, 1968, 1977; Hempel, 1985; Stonehouse, 1989; Smith, 1990a, 1990b; Dayton *et al.*, 1994). Similarities and differences between the modern polar regions are informative (Table I), but regional historical processes were probably more important in determining the nature of the two fish faunas than were aspects of the modern environment. Faunal composition and diversity are known to be strongly linked to geologic history (Brey *et al.*, 1994).

As events leading to the isolation and cooling of the Southern Ocean during the Cenozoic have recently been synthesized with respect to fish (Eastman, 1993), I will briefly summarize what happened during this time in the Arctic (Kennett, 1982; Barry, 1989; Dayton, 1990). As in the south, tectonic changes during the Tertiary produced

shifts in ocean circulation and climate. Although Europe began to separate from Greenland in the late Cretaceous, the exchange of Atlantic and Arctic waters through the passage between Greenland and Svalbard was not possible until 27 million years ago (mya). This passage remained narrow into the Pliocene. The Arctic Region was in a high latitude position by the early Tertiary, but the climate remained temperate with water temperatures of 10-15°C. Waters cooled gradually through the Eocene and Oligocene. Arctic land masses reached their present positions and temperatures dropped below freezing during the Miocene about 10-15 mya. Additional Miocene cooling and ice sheet expansion in the south resulted in lower sea levels in the north and the emergence of the Bering land bridge which isolated the Arctic and Pacific Oceans. Because oceanic circulation was latitudinal at this time, there was little faunal exchange between the Arctic and Atlantic Oceans. The closure of the Isthmus of Panama about 3.2 mya strengthened the Gulf Stream and increased precipitation at high latitudes thereby contributing to ice sheet development. This late Pliocene ice sheet development in the Northern Hemisphere lagged about 10 million years behind that in the Antarctic. The Atlantic and Pacific Oceans had connections to the Arctic at this time and faunal interchange was possible. The Bering Strait link to the Arctic Ocean has existed during interglacial times of high sea level since about 2.2 mya. Beginning 2 mya, the Pleistocene was marked by glacial advances and retreats with periodic freshwater input to the Arctic basin. There are conflicting views about when cooling led to the formation of Arctic sea ice. Permanent ice cover has been present for at least 0.7 mya, although intermittent ice cover may have existed as long as 2.0 mya. Estuarine and freshwater habitats were available to fishes during interglacial periods, including the most recent which began 6-14,000 years ago. Some components of the Arctic marine fauna may have persisted from the Miocene and Pliocene, but exchanges with the Atlantic and Pacific were also possible during more recent marine transgressions.

Table I. - Comparison of physical and biological characteristics of the polar oceans (modified from Knox and Lowry, 1977; Hempel, 1985; Stonehouse, 1989; Dayton, 1990).

Feature	Southern Ocean	Arctic Ocean
Geographic disposition	Surrounds Antarctica between 50 and 70°S	Enclosed by land between 70 and 80°N
Area	35-38 x 10⁶ km²	14.6 x 10⁶ km²
Extent of continental shelf	Narrow, few islands	Broad, extensive archipelagos
Depth of continental shelf	400-600 m	100-500 m
Shelf continuity with ocean	Widely open to three oceans	Open only at Fram and Bering Straits
Direction of currents	Circumpolar	Transpolar
Upwelling and vertical mixing	Extensive	Little
Nutrient availability	Continuously high	Seasonally depleted
Seasonality of solar illumination	Weak	Strong
Primary productivity	Moderate to high	Moderate
Fluvial input to ocean	None	Extensive
Salinity at 100-150 m	34.5-34.7‰	30-32‰
Seasonality of pack ice	High	Low
Physical disturbance of benthos by large predators	Low	Extensive

Modern

The modern Arctic Ocean contains two basins and is fringed by marginal seas adjacent to the continental land masses. It is covered for most of the year by a 3-4 m thick layer of sea ice. The western Arctic continental shelf from Alaska to Greenland is relatively narrow, but the eastern shelf is 600-800 km wide from Spitsbergen eastward through the Barents, Kara, Laptev, East Siberian and Chukchi Seas. The broad, shallow (150 m) shelves of these marginal Eurasian seas are associated with the outflow of major rivers, and constitute 35% of the area of the Arctic basin. All shelves and slopes together account for 68% of the area of the Arctic Ocean, consequently the average depth is only 1,117 m compared to the oceanic average of about 3,700 m. Since the Arctic Ocean is landlocked and receives considerable river discharge, the salinity is lower than that of the world ocean.

Water from the world ocean flows into the Arctic basin through two passageways. The high volume West Spitsbergen Current introduces North Atlantic water into the Arctic Ocean through the Fram Strait between Spitsbergen and northern Greenland. This flow encompasses depths of 200-2,000 m and therefore provides access to the Arctic for both shallow and deep water fish. The main outflow from the Arctic is also through the Fram Strait via the East Greenland Current. There is also flow of North Pacific water from the Bering Sea into the Chukchi Sea through the shallow (50 m) and narrow Bering Strait. It probably excludes all but the most shallow living fish. Flow is about one-fiftieth the volume of that entering from the Atlantic. North temperate fish have access to the Arctic through these two passages and the shelf continuities, but wide dispersal of fish larvae is less likely than in the Antarctic because of the separation of the basins and the absence of a circumpolar current involving the entire Arctic Region.

As far as zoogeographic regions and fish faunas are concerned, I will utilize the Antarctic Region recognized in *Fishes of the Southern Ocean* (Gon and Heemstra, 1990), basically the area south of the Antarctic Polar Front modified to conform to the CCAMLR Convention Area. The region includes the Subantarctic islands in the Indian Ocean Sector. The zoogeographic boundary of the Arctic Region is less distinct. Following Andriashev and Chernova (1995), it includes the Arctic Ocean and its named seas. It extends southward in the North Atlantic to include Labrador, Greenland, northern Iceland, the Norwegian Sea and the Barents Sea. In the North Pacific it includes the northern Bering Sea south to Cape Navarin, St. Lawrence Island and the mouth of the Yukon River (62-63°N).

THE FISH FAUNAS

Taxonomic comparison

Tables II and III summarize the taxonomic composition of the two faunas. Higher taxonomic categories and phylogenetic sequencing are based on Nelson (1994). The Antarctic fauna includes 274 species representing 49 families; the Arctic fauna 416 species in 96 families, about 52% larger in terms of species composition. If the figure for recognition of dominant faunal elements is arbitrarily set at 5%, only five groups account for about 74% of the Antarctic fauna (notothenioids, myctophids, liparids, zoarcids and gadiforms). With 35% of the species, notothenioids prevail in this assemblage. In the Arctic six dominant groups comprise 58% of the fauna (zoarcoids, gadiforms, cottids, salmonids, pleuronectiforms and chondrichthyans). Only gadiforms and zoarcids are

Table II. - Taxonomic comparison by families of the fish faunas of the Antarctic and Arctic Regions. Taxonomic categories and phylogenetic sequencing are according to Nelson (1994). Antarctic species from Eastman (1993), slightly modified from Gon and Heemstra (1990). Emendations to current list, i.e., differences from Eastman (1993), include removal of the nototheniid *Lepidonotothen kempi* (synonymized with *L. squamifrons* by Schneppenheim *et al.*, 1994) and addition of a new bathydraconid (Skóra, 1995). Therefore total number of Antarctic species remains at 274. Arctic species from Andriashev and Chernova (1995).

Taxon	Antarctic No. of spp. (% of fauna)	Arctic No. of spp. (% of fauna)
Superclass Agnatha		
Class Myxini		
Order Myxiniformes		
Myxinidae (hagfishes)	1 (0.4)	1 (0.2)
Class Cephalaspidomorphi		
Order Petromyzontiformes		
Petromyzontidae (lampreys)	1 (0.4)	3 (0.8)
Superclass Gnathostomata		
Class Chondrichthyes		
Order Chimaeriformes		
Chimaeridae (ratfishes)	—	2 (0.5)
Order Carcharhiniformes		
Scyliorhinidae (cat sharks)	—	1 (0.2)
Triakidae (hound sharks)	—	1 (0.2)
Carcharhinidae (requiem sharks)	—	1 (0.2)
Order Lamniformes		
Cetorhinidae (basking shark)	—	1 (0.2)
Lamnidae (mackerel sharks)	1 (0.4)	3 (0.8)
Order Hexanchiformes		
Chlamydoselachidae (frill shark)	—	1 (0.2)
Order Squaliformes		
Dalatiidae (sleeper sharks)	2 (0.7)	4 (1.1)
Squalidae (spiny dogfishes)	—	1 (0.2)
Order Rajiformes		
Rajidae (skates)	8 (2.9)	11 (2.6)
Class Actinopterygii		
Order Acipenseriformes		
Acipenseridae (sturgeons)	—	4 (1.1)

Taxon	Antarctic No. of spp. (% of fauna)	Arctic No. of spp. (% of fauna)
Order Albuliformes		
Halosauridae (halosaurs)	1 (0.4)	—
Notacanthidae (spiny eels)	1 (0.4)	2 (0.5)
Order Anguilliformes		
Anguillidae (freshwater eels)	—	2 (0.5)
Synaphobranchidae (cutthroat eels)	2 (0.7)	2 (0.5)
Nemichthyidae (snipe eels)	—	1 (0.2)
Serrivomeridae (sawtooth eels)	—	1 (0.2)
Order Saccopharyngiformes		
Saccopharyngidae (swallowers)	—	1 (0.2)
Order Clupeiformes		
Clupeidae (herrings)	—	5 (1.3)
Superorder Ostariophysi		
Order Cypriniformes		
Catostomidae (suckers)	—	1 (0.2)
Superorder Protacanthopterygii		
Order Esociformes		
Esocidae (pikes)	—	1 (0.2)
Order Osmeriformes		
Argentinidae (argentines)	—	1 (0.2)
Microstomatidae (microstomatids)	1 (0.4)	1 (0.2)
Bathylagidae (deep-sea smelts)	3 (1.1)	—
Alepocephalidae (slickheads)	4 (1.4)	4 (1.1)
Platytroctidae (tubeshoulders)	1 (0.4)	7 (1.7)
Osmeridae (smelts)	—	7 (1.7)
Order Salmoniformes		
Salmonidae (salmonids)	—	32 (7.7)

Table II. - Continued 1.

Taxon	Antarctic No. of spp. (% of fauna)	Arctic No. of spp. (% of fauna)
Superorder Stenopterygii		
Order Stomiiformes		
Gonostomatidae (bristlemouths)	5 (1.8)	4 (1.1)
Sternoptychidae (hatchetfishes)	2 (0.7)	6 (1.4)
Stomiidae (barbeled dragonfishes)	5 (1.8)	3 (0.8)
Superorder Cyclosquamata		
Order Aulopiformes		
Scopelarchidae (pearleyes)	2 (0.7)	—
Notosudidae (waryfishes)	1 (0.4)	1 (0.2)
Synodontidae (lizardfishes)	—	1 (0.2)
Paralepididae (barracudinas)	4 (1.4)	3 (0.8)
Anotopteridae (daggertooths)	1 (0.4)	1 (0.2)
Alepisauridae (lancetfishes)	1 (0.4)	1 (0.2)
Superorder Scopelomorpha		
Order Myctophiformes		
Myctophidae (lanternfishes)	35 (12.7)	7 (1.7)
Superorder Lampridiomorpha		
Order Lampriformes		
Lamprididae (opahs)	2 (0.7)	1 (0.2)
Trachipteridae (ribbonfishes)	—	1 (0.2)
Regalecidae (oarfishes)	—	1 (0.2)
Superorder Paracanthopterygi		
Order Ophidiiformes		
Carapidae (carapids)	1 (0.4)	—
Ophidiidae (cusk-eels)	1 (0.4)	—
Bythitidae (viviparous brotulas)	—	1 (0.2)
Order Gadiformes		
Macrouridae (grenadiers)	11 (4.0)	5 (1.3)

Taxon	Antarctic No. of spp. (% of fauna)	Arctic No. of spp. (% of fauna)
Moridae (morid cods)	4 (1.4)	3 (0.7)
Melanonidae (melanonids)	1 (0.4)	—
Muraenolepididae (eel cods)	4 (1.4)	—
Phycidae (phycod hakes)	—	4 (1.1)
Merlucciidae (merluccid hakes)	—	2 (0.5)
Gadidae (cods)	1 (0.4)	30 (7.2)
Order Lophiiformes		
Lophiidae (goosefishes)	—	1 (0.2)
Antennariidae (frogfishes)	—	1 (0.2)
Caulophrynidae	—	1 (0.2)
Melanocetidae (devil-anglers)	1 (0.4)	—
Himantolophidae (footballfishes)	—	1 (0.2)
Oneirodidae (dreamers)	1 (0.4)	5 (1.3)
Ceratiidae (seadevils)	1 (0.4)	2 (0.5)
Gigantactinidae	—	1 (0.2)
Linophrynidae	—	2 (0.5)
Order Beloniformes		
Belonidae (needlefishes)	—	1 (0.2)
Scomberesocidae (sauries)	—	1 (0.2)
Superorder Acanthopterygii		
Order Stephanoberyciformes		
Melamphaidae (bigscale fishes)	3 (1.1)	1 (0.2)
Cetomimidae (flabby whalefishes)	3 (1.1)	—
Order Beryciformes		
Anoplogastridae (fangtooths)	—	1 (0.2)
Diretmidae (spinyfins)	—	1 (0.2)
Berycidae (alfonsinos)	—	1 (0.2)

Table II. - Continued 2.

Taxon	Antarctic No. of spp. (% of fauna)	Arctic No. of spp. (% of fauna)
Order Zeiformes		
Orcosomatidae (oreos)	1 (0.4)	—
Order Gasterosteiformes		
Gasterosteidae (sticklebacks)	—	3 (0.8)
Syngnathidae (pipefishes)	—	2 (0.5)
Order Scorpaeniformes		
Scorpaenidae (scorpionfishes)	1 (0.4)	6 (1.4)
Congiopodidae (racehorses)	—	—
Triglidae (searobins)	—	1 (0.2)
Hexagrammidae (greenlings)	—	2 (0.5)
Cottidae (sculpins)	—	44 (10.6)
Hemitripteridae	—	1 (0.2)
Agonidae (poachers)	—	12 (2.9)
Psychrolutidae (fathead sculpins)	—	6 (1.4)
Cyclopteridae (lumpfishes)	—	10 (2.4)
Liparidae (snailfishes)	31 (11.3)	17 (4.1)
Order Perciformes		
Suborder Percoidei		
Moronidae (temperate basses)	—	1 (0.2)
Percidae (perches)	—	2 (0.5)
Bramidae (pomfrets)	—	3 (0.8)
Caristiidae (manefishes)	—	1 (0.2)
Suborder Zoarcoidei		
Zoarcidae (eelpouts)	22 (8.0)	40 (9.6)
Stichaeidae (pricklebacks)	—	17 (4.1)
Cryptacanthodidae (wrymouths)	—	1 (0.2)
Pholidae (gunnels)	—	3 (0.8)
Anarhichadidae (wolffishes)	—	5 (1.3)
Zaproridae (prowfish)	—	1 (0.2)

Taxon	Antarctic No. of spp. (% of fauna)	Arctic No. of spp. (% of fauna)
Suborder Notothenioidei		
Bovichtidae (thornfishes)	1 (0.4)	—
Nototheniidae (notothens)	33 (12.0)	—
Harpagiferidae (spiny plunderfishes)	6 (2.2)	—
Artedidraconidae (plunderfishes)	24 (8.7)	—
Bathydraconidae (dragonfishes)	16 (5.8)	—
Channichthyidae (icefishes)	15 (5.4)	—
Suborder Trachinoidei		
Chiasmodontidae	—	1 (0.2)
Ammodytidae (sand lances)	—	6 (1.4)
Suborder Blennioidei		
Tripterygiidae (triplefins)	1 (0.4)	—
Suborder Scombroidei		
Gempylidae (snake mackerels)	1 (0.4)	—
Trichiuridae (cutlassfishes)	—	1 (0.2)
Scombridae (mackerels & tunas)	1 (0.4)	2 (0.5)
Xiphiidae (billfishes)	—	1 (0.2)
Suborder Stromateoidei		
Centrolophidae (driftfishes)	1 (0.4)	1 (0.2)
Order Pleuronectiformes		
Achiropsettidae (southern flounders)	4 (1.4)	—
Scophthalmidae	—	2 (0.5)
Pleuronectidae (righteye flounders)	—	26 (6.3)
Order Tetraodontiformes		
Molidae (molas)	—	1 (0.2)
TOTALS	274 (100%)	416 (100%)

common to both regions at the 5% level of dominance. If this requirement is relaxed to include components that reach the 5% level in either region (Table III), a total of six groups are shared between the two faunas and seven groups contribute about 80% of the Antarctic fauna and eight groups provide about 64% of the Arctic fauna.

Ignoring percentages and restricting the analysis to the coldest water at the highest latitudes (> 65°S and N), only zoarcids and liparids are common to both faunas. There are 40 Arctic (Andriashev and Chernova, 1995) and 22 Antarctic zoarcids (Anderson, 1990). There are 17 Arctic liparids and, as of 1990, there are thirty-one species in the Antarctic (Stein and Andriashev, 1990). However with an additional 59 species recently described or presently under description, the Antarctic liparids number about 90 species (Andriashev, 1996), surpassing the Nototheniidae as the most speciose fish family in the Southern Ocean. Liparids, however, do not approach the ecological or morphological diversity of nototheniids, nor do they dominate the fish biomass as do nototheniids in shelf and slope waters.

Despite the geographic separation, different zoogeographic histories and ages of the two polar ecosystems, it is of interest that 27 families, 35 genera and 10 species are common to both. It must be noted, however, that most of these genera and species are members of widely distributed bathypelagic, epibenthic or benthic families that have cosmopolitan distributions in the deep cold oceans of the world. They therefore provide little zoogeographic insight into the evolution of the endemic high latitude shelf faunas. Many are found only at the periphery of the polar regions. These shared genera are dominated by stomiiforms, aulopiforms, myctophiforms, gadiforms, liparids and zoarcids.

In comparing the taxonomic composition of the two faunas, the most obvious difference is that no single group in the Arctic dominates the fauna as do the Antarctic notothenioids with 35% of the species. In the Arctic, scorpaeniforms come closest to dominance with a total of 99 species in nine families, about 24% of the total fauna (Table II). Scorpaeniforms are a benthic, predominantly marine group, especially diverse in the Northern Hemisphere and North Pacific Ocean.

Table III. - Major taxonomic components of the fish faunas of the Antarctic and Arctic Regions based on table II. Groups listed contain at least 5% of the species in either the Antarctic or Arctic.

Taxon	Antarctic No. of spp. (% of fauna)	Arctic No. of spp. (% of fauna)
Class Chondrichthyes	11 (4.0%)	26 (6.3%)
Class Actinopterygii		
Order Salmoniformes	---	32 (7.7%)
Myctophiformes	35 (12.7%)	7 (1.7%)
Gadiformes	21 (7.7%)	44 (10.6%)
Scorpaeniformes		
Cottidae	---	44 (10.6%)
Liparidae	31 (11.3%)	17 (4.1%)
Perciformes		
Zoarcoidei	22 (8.0%)	67 (16.1%)
Notothenioidei	95 (34.7%)	---
Pleuronectiformes	4 (1.4%)	28 (6.7%)
Totals	219/274 = (79.9%)	265/416 = (63.8%)

Another fact emerging from table II is that the Arctic fauna has a wider taxonomic representation, especially among the phyletically primitive actinopterygians many of which are euryhaline. With the availability of freshwater and brackish habitats in the Arctic, 14% (58/416) of the species are either diadromous (usually anadromous) or freshwater. Dominant in this component of the Arctic fauna are acipenserids, anguillids, clupeids, catostomids, esocids, osmerids and salmonids. This is a relatively young (post-Pleistocene) element of the fauna that immigrated into newly developing lakes and river systems after the glacial retreat 6-14,000 years ago. Euryhalinity has been an important factor in determining the distribution of groups like the salmonids in the Arctic. Conversely, salinity tolerance has played no role in determining the make-up of the modern high latitude Antarctic fauna (although a few notothenioids have invaded brackish and freshwater, low diversity habitats in Australia and South America). Freshwater habitats for fish do not exist in modern Antarctica.

In comparing species endemism between the two regions, the incidence is considerably higher in the Antarctic, and this is to be expected because of the isolation and greater age of the ecosystem. Here species endemism stands at 88% for the benthic fauna of the shelf and upper slope (174 species) and rises to 97% when only notothenioids are considered (Andriashev, 1987). Species endemism for marine fish in the Arctic is 20-25% (Briggs, 1974, p. 290). Endemism in the Arctic is also low to non-existent in higher taxonomic categories like genera and families, another reflection of the young age of the fauna. In the Antarctic, however, six of 49 families (12%) are endemic (Harpagiferidae, Artedidraconidae, Bathydraconidae, Channichthyidae, Muraenolepididae and Achiropsettidae).

Evolutionary comparison
Antarctic fish

Comparing numbers of species or scaling the number of species to the size of the ecosystem imparts little appreciation for the unique aspects of the history and biology of Antarctic and Arctic fishes. An alternative approach involves recognizing that the two polar ecosystems differ in geological age and have been subject to different historical processes that shaped the environment and composition of the fauna (Table IV). Given the scarcity of prime fish habitats, is it remarkable that diversity in the Antarctic is as great as it is. There are no lakes, rivers, deltas, estuaries, coral reefs, intertidal or shallow shelf habitats and the epipelagic zone (< 200 m) is nearly uninhabited, but there are 174 species of fish on the shelf and upper slope.

Table IV. - A broad comparison of the polar fish faunas.

Feature	Antarctic region	Arctic region
Number of families	49	96
Number of species (freshwater/marine)	274 (0/274)	416 (58/358)
Species endemism for freshwater fish	---	Very low (2%)
Age of freshwater ecosystem (my)	---	0.01-0.1
Species endemism for marine fish	High (88%)	Low (20-25%)
Generic endemism for marine fish	High (76%)	0%
Familial endemism for marine fish	High (12%)	0%
Age of marine ecosystem (my)	13-22	0.7-2.0
Faunal boundaries	Distinct	Indistinct
Adaptive radiation of an old indigenous faunal element	Yes	No

Dominant among this assemblage are the notothenioids, the only known example of an adaptive radiation of fish in a marine habitat. Although the Antarctic fauna is usually described as holding lower species diversity than the Arctic fauna, the ecological and morphological diversity in the family Nototheniidae far exceeds that of the entire high Arctic fauna. The original notothenioid stock was an indigenous element of the Gondwanan shelf since the early Tertiary, and possibly extended back into the late Cretaceous. They became associated with the Antarctic plate and evolved with the Antarctic ecosystem. The beginning of the notothenioid radiation is hypothesized to have begun about 22 mya, when a portion of the stock became isolated in the cooling Southern Ocean south of the developing Antarctic Polar Front. Sea ice probably appeared about 12-14 mya. While it may be generally true that the Antarctic has the oldest and most isolated assemblage of marine species in the world (Dayton et al., 1994, p. 98), molecular divergence times suggest that the diversification of high latitude notothenioids took place relatively recently, between 10-15 and 2.5 mya (Bargelloni et al., 1994; Ritchie et al., 1996).

Because of the isolation, low water temperatures and current patterns, there have been few immigrants joining the modern fauna from other southern continents. Notothenioids like Patagonotothen, on the other hand, seem to have dispersed northward into depauperate areas of adjacent South America. The original notothenioid stock also left behind phyletically primitive elements that diverged prior to the isolation of Antarctica. These include Pseudaphritis urvillii in Australia and Eleginops maclovinus in South America. Finally, the faunal boundaries between the Antarctic and Subantarctic faunas are distinct, unlike the situation in the Arctic.

Arctic fish

The Arctic fauna has a different taxonomic composition and is considerably younger with less endemism than the Antarctic fauna. It consists of boreal marine and freshwater fish which are generally more eurythermal and euryhaline than their Antarctic counterparts (Tables IV, V). The high latitude Arctic marine fauna is of low species diversity (only 75 of 416 species, or 18%, are Arctic and predominantly Arctic species according to Andriashev and Chernova, 1995), and it is only when the more widely distributed boreal elements are added that the number approaches 416 species. These 75 Arctic species are predominantly (81%) zoarcids (21 species), salmonids (17 species), liparids (10 species), cottids (8 species) and gadids (5 species). The Zoarcidae and Liparidae, the only two families well represented in the highest latitudes of both polar regions, are good groups for

Table V. - Comparison of phyletically unrelated cryopelagic polar fish (with Boreogadus, Arctogadus and Eleginus included among the Arctic gadids). References given in text.

Feature	Antarctic Pagothenia	Arctic gadids
Phyletic position within family	Derived	Derived
Swim bladder	Absent	Present
Typical habitat temperature	-1.9°C	-1.9 to +6.2°C
Antifreeze glycotripeptide: monomeric repeat of (Thr-Ala/Pro-Ala-)$_n$	Present (3.5%)	Present (?%)
Serum osmolality	570 mosmol.kg^{-1}	590 mosmol.kg^{-1}
Salinity tolerance	Stenohaline	Euryhaline (0-32%$_c$)
Glomerular development	Aglomerular	Aglomerular or glomerular

comparative studies. The Arctic fauna has no endemic higher taxonomic category equivalent to the Antarctic notothenioids and there has been no comparable adaptive radiation of any fish group.

Faunal boundaries between the Arctic, Subarctic and boreal faunas are not distinct. Or stated in a slightly different way, all the families comprising the Arctic fauna are also represented in the North Temperate Region. Employing data from Bering Sea fishes to further emphasize this point, Ekman (1953) notes that the sharp zoogeographic boundary for the shelf fauna falls between the temperate and subtropical/tropical regions (only 38% familial similarity), not between the temperate and Arctic/boreal regions (100% familial similarity). The North Atlantic and North Pacific character of the Arctic fauna reflects the continuity of shelf areas between the Arctic/boreal and temperate regions.

Another indication of the relatively young age of the Arctic fauna is the paucity of endemic species among the freshwater and anadromous fish. There is only one endemic subspecies, for example, among the 101 native boreal freshwater species of Hudson Bay, Ungava Bay and the Arctic Archipelago drainages (Crossman and McAllister, 1986). For the entire high Arctic freshwater and anadromous fauna, endemicity is about 2% and is confined primarily to whitefishes of the salmonid genus *Coregonus* (Andriashev and Chernova, 1995). Cycles of glaciation and deglaciation commenced about 100,000 years ago. Since the last deglaciation began about 14,000 years ago and ended 6,000 years ago (Dunton, 1992), the freshwater fauna cannot be much older than this (late Pleistocene to post-Pleistocene).

Although the freshwater component of the modern Arctic fauna is young, some of the marine components are representatives of groups composing the cosmopolitan Tethyan fauna of the late Cretaceous. Gadiforms, for example, may have originated in boreal Atlantic waters during the Cretaceous (Svetovidov, 1948), and a fossil gadiform is present in the Paleocene of Greenland (Cohen, 1984). Zoarcids (Anderson, 1994) and liparids (Andriashev, 1986, 1991) are also old elements of the Arctic marine fauna. Both groups are thought to have originated in the North Pacific during the Eocene. Only shallow living North Pacific liparid genera were able to penetrate the Bering Strait and colonize the Arctic and then the North Atlantic during Pliocene marine transgressions (Andriashev, 1991). Liparids and zoarcids probably dispersed into the Southern Hemisphere via deep waters during the Miocene. In the south they underwent radiations and became important components of the Antarctic fauna. Sometime after the opening of the Drake Passage in the Miocene (22-25 mya), deep living liparid genera (*Paraliparis* and *Careproctus*) were able to disperse to the North Atlantic and Arctic via the Mid-Atlantic Ridge and continental slope (Andriashev, 1991). Some zoarcids (*Melanostigma*) also spread back into boreal waters after originating in South American-Antarctic waters (Anderson, 1994).

The cryopelagic gadids associated with the undersurface of the sea ice are a distinguishing, but younger, gadiform component of the high Arctic marine fauna. Perennial ice cover in the Arctic Ocean is thought to have developed 0.7-2.0 mya (Dunton, 1992), so this is an approximate maximum age for the cryopelagic gadids.

COMMON EVOLUTIONARY THEMES AT
VARIOUS LEVELS OF DIVERSITY

Although the geological histories of the regions and the taxonomic composition of the faunas are different, there are convergent evolutionary trends among Antarctic and

Arctic species that share habitat similarities. Below are examples suggesting that these trends have occurred at the intraspecific, specific and ecological levels of diversity, however parallel examples involving both faunas are not evident at all levels.

Appearance of intraspecific morphs in low diversity habitats

Intraspecific trophic or habitat morphs have appeared in geologically young habitats in both polar regions. In the shallow (< 20 m) inshore waters of McMurdo Sound there is a phenotypically plastic population of *Trematomus newnesi*, with two distinct morphs easily separated by visual inspection: a typical morph and a large mouth/broad headed morph comprising 28% of the population (Eastman and DeVries, 1997). The large mouth morph has a wider and blunter head, longer upper jaw, wider gape, more heavily ossified jaws and darker coloration. Inferences from morphology and measurements suggest that the large mouth morph is more benthic than the typical semipelagic morph. Heterochrony may be responsible for the differences in morphology. Study of genetic diversification has not yet been undertaken. This is the first clear example of a trophic or habitat morph in any species of marine fish. The discovery of this phenotypic plasticity reveals another aspect of fish diversity in high Antarctic shelf waters and extends the bounds of the nototheniid adaptive radiation to the intraspecific level.

The Arctic char, *Salvelinus alpinus*, resembles *T. newnesi* in having a high latitude circumpolar distribution. The population in Lake Hazen (82°N), Ellesmere Island, Northwest Territories is the most northerly of any freshwater fish (Nelson, 1994, p. 192). This species has repeatedly diversified into benthic and limnetic morphs in postglacial Arctic and boreal lakes with few fishes (Skúlason and Smith, 1995). These morphs differ in size, coloration, feeding habits and position in the water column. At first glance these lakes appear to share few biological characteristics with the nearshore Antarctic marine environment inhabited by *T. newnesi*. However, reduced competition associated with a low diversity fish fauna may be a common factor in the origin of intraspecific morphs in both *S. alpinus* and *T. newnesi*. The High Antarctic shelf is like some lakes in that it is isolated and cut off from migration. Trophic and morphological diversification predominate in species-poor fish communities, suggesting that the absence of competition allows niche expansion (Robinson and Wilson, 1994, p. 604). This is consistent with Dunbar's (1968) suggestion that intraspecific variants or morphs are more common in polar and temperate latitudes than in the tropics or subtropics. This phenomenon reflects the immaturity of polar ecosystems, with morphs as evidence of continuing development or diversification within the ecosystem.

Organismal or species diversity: an adaptive radiation

At the species or organismal level, neither polar fauna is very diverse if species are simply counted and compared to the number of fish in temperate or tropical regions. However the Antarctic suborder Notothenioidei, and especially the family Nototheniidae, are adaptive radiations of about 120 and 50 species, respectively (Eastman, 1993; Clarke and Johnston, 1996; Klingenberg and Ekau, 1996). This is the only known example of an adaptive radiation among marine fish. Notothenioids are overwhelmingly dominant by both number and biomass in most shelf and upper slope areas of the Southern Ocean. Although lacking swim bladders, they exhibit considerable ecological and morphological diversity and occupy most benthic and water column habitats.

There has been no adaptive radiation of fish in the Arctic, but the evolutionary time frame has been shorter and tectonic events have not isolated the northern land mas-

ses and their continental shelves. Since major radiations usually take time, it is possible that, given additional millions of years, benthic groups like gadids or cottids could radiate to occupy a position of dominance equivalent to nototheniids in the Antarctic. With 25-30 species, the radiation of swim bladderless cottids in Lake Baikal provides evidence that this is within the realm of possibility. Lake Baikal is, however, at least 20 million years older than the modern Arctic ecosystem.

Similar ecological or community diversity: water column habitats

At the ecological or community level, there are equivalent species in pelagic and cryopelagic water column habitats at both poles. Again regional historical factors have played an important role in initiating this trend. In the Arctic glacial advances resulted in several significant drops in sea level. Large areas of the shelf were exposed and the shelf fauna was eradicated (Dunton, 1992). The Antarctic ice sheet has scoured at least parts of the shelf, eliminating some fish species or driving them to refuge in deeper water. Thus the diversification of water column species in both oceans probably reflects the past instability of the shelf as a habitat for fishes, the productivity in certain areas of the water column and the underutilization of this habitat by pelagic fishes.

Pelagic species

These water column species are few in number but ecologically important, especially *Pleuragramma antarcticum* in the high Antarctic. This keystone species dominates the biomass in the water column in areas such as the Weddell Sea (Hubold, 1984). When considering the evolution of the polar faunas, the Antarctic species are unusual as they are descended from a stock without swim bladders, and they are therefore designated as secondarily pelagic. Seventeen species or about 50% of the nototheniids from the Antarctic region are non-benthic as adults (Eastman, 1993). These water column lifestyles encompass the pelagic, cryopelagic, semipelagic and epibenthic habitats.

There is no evolutionary equivalent to *Pleuragramma antarcticum* in the high Arctic. There are ecologically similar species that feed on euphausiids, the clupeid *Clupea harengus* and the osmerid *Mallotus villosus*. But both are predominantly boreal Pacific and Atlantic rather true Arctic species (Andriashev and Chernova, 1995). Both are primarily pelagic members of water column families possessing swim bladders. Therefore, unlike *Pleuragramma antarcticum*, they have not experienced evolutionary alteration of their morphology in attaining neutral buoyancy.

Cryopelagic species

Permanent ice cover is characteristic of the highest latitudes of both polar seas. The undersurface of the ice, the cryopelagic habitat, is a site of significant primary productivity and a point of refuge for a variety of organisms including fish (Andriashev, 1970). Although phyletically unrelated, the cryopelagic fish of the two regions have an ecologically similar association with the ice-water interface (Table V). Cryopelagic species include Antarctic nototheniids of the genus *Pagothenia* and the Arctic gadids *Boreogadus saida* (polar cod) and *Arctogadus glacialis* (Arctic cod). *Boreogadus* and *Arctogadus* are the most phyletically derived gadid genera (Howes, 1991). *Pagothenia* is phyletically derived, but its position within the trematomid radiation is uncertain (Bargelloni *et al.*, 1994; Ritchie *et al.*, 1996; Klingenberg and Ekau, 1996).

Physiological similarities and differences among cryopelagic species

Antifreeze is necessary for the survival of fish in ice laden polar water throughout the year and in some boreal marine habitats during the winter. Various types of antifreeze glycopeptides and peptides have appeared in polar fish (DeVries, 1988; Cheng and De-Vries, 1991; Davies *et al.*, 1993; Wöhrmann, 1993, 1996). The cryopelagic nototheniids and gadids possess an identical antifreeze glycopeptide.

More structural diversity in antifreeze peptides is present in Arctic than Antarctic fish, but this probably reflects their greater taxonomic diversity. One of the most divergent strategies is seen in the rainbow smelt *Osmerus mordax*. In addition to possessing type II antifreeze peptide, this species employs an additional suite of osmolytes to enhance freezing resistance including glycerol, urea and trimethylamine oxide (Raymond, 1992, 1993, 1994, 1995).

In addition to subzero temperatures and ice, Arctic and boreal gadids, unlike Antarctic fish, must also accommodate to changes in salinity and temperature during their life cycle which may involve anadromy (Andriashev, 1954). These is even true in the case of *Boreogadus saida* which has been captured under the ice close to the North Pole (Andriashev, 1954, p. 197). Although *B. saida* from Spitsbergen have antifreeze (A.L. DeVries, unpubl. data) and aglomerular kidneys (Christiansen *et al.*, 1996; J.T. Eastman and A.L. DeVries, unpubl. data), this species can tolerate freshwater and temperatures as high as 6.2°C (Svetovidov, 1948).

In considering Arctic gadids, inclusion of *Eleginus gracilis* (saffron cod) and *E. navaga* (navaga) is informative because they provide some appreciation of the physiological variability in the family (Table V). Arctic and boreal gadids exhibit more physiological plasticity, with less specialization of organ systems toward low and constant temperatures and salinity as is the case in Antarctic nototheniids. For example, the pauciglomerular kidneys of *Eleginus gracilis* (Eastman *et al.*, 1987) show seasonal variability in glomerular structure in Japanese waters (Kitagawa *et al.*, 1990). In the winter the glomeruli are atrophic, small in diameter with no blood cells in the capillaries. As in Antarctic species, the plasma osmolality is also elevated in *Eleginus navaga* (navaga) from the White Sea. This makes the fish isosmotic, but in 20‰ seawater rather than full strength seawater (Christiansen *et al.*, 1995).

It is interesting that recent acclimatization studies at McMurdo Sound, where temperature and salinity are constant, have shown that osmoregulatory organs of trematomids are also capable of responding to temperature change. Gonzalez-Cabrera *et al.* (1995) found that 35 days of acclimatization at 4°C induced a decrease of about 150 mosmol kg^{-1} in serum osmolality which resulted from a positive compensation of Na$^+$/K$^+$-ATPase activity in the gill and kidney.

CONCLUSION

Drawing an analogy with a protocol in experimental biology, the fish faunas in the polar regions can be considered to be the results of two evolutionary experiments. Each has a starting point, a time course, sampling points at occasional intervals and a termination point that allows examination of the results of the experiments, the modern polar faunas. The experiments began during the late Cretaceous/early Tertiary when the fish of the world ocean had a cosmopolitan distribution and distinct polar biotas did not exist. The experiments ran for tens of millions of years during which geologic and climatic changes (vicariant events) led to different degrees of continental isolation, to cooling

of the oceans and to cycles of glaciation and deglaciation. These events did not occur simultaneously at both poles. Times of habitat instability may have been more important in promoting diversification of fish than were long periods of stasis. The analogy with an experiment begins to break down here because these vicariant events represent uncontrolled variables that led to the diversification of the faunas. Such variables would be undesirable in a typical experiment, but they are essential in evolutionary events. Sampling intervals, for a glimpse at the preliminary results of the experiments, are provided by the fossil record. These are meager for the Antarctic (late Cretaceous, late Eocene and Pliocene) and non-existent for the younger Arctic fauna, and unfortunately the fossils provide little understanding of the transformation from temperate to modern polar faunas. At the termination of the experiments, we find that although the modern polar environments share some physical and biological characteristics, the taxonomic composition and the biology of the fish faunas are very different. It is to be expected that the outcomes of different evolutionary situations will be different.

Geologically old, isolated environments frequently have unusual faunas. The Antarctic fauna, with its adaptive radiation of fish, is just as unique, but not as well publicized, as faunas of Lake Baikal or the East African Great Lakes. The members of the European Science Foundation Network on Fishes of the Antarctic Ocean are examining the consequences of the notothenioid radiation at levels of biological organization ranging from molecules to organisms. An increasing number of biologists are becoming aware of this work, of the nature of the notothenioid radiation and of Antarctic shelf waters as an fascinating evolutionary site.

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